

Title	The Ascidians of the Japan Sea. III
Author(s)	Nishikawa, Teruaki
Citation	PUBLICATIONS OF THE SETO MARINE BIOLOGICAL LABORATORY (1992), 35(6): 303-334
Issue Date	1992-11-30
URL	<a href="http://hdl.handle.net/2433/176214">http://hdl.handle.net/2433/176214</a>
Right	
Type	Departmental Bulletin Paper
Textversion	publisher

# The Ascidians of the Japan Sea. III<sup>1)</sup>

TERUAKI NISHIKAWA

Biological Laboratory, College of General Education<sup>2)</sup>, Nagoya University,  
Chikusa-ku, Nagoya 464-01, Japan

---

*With Text-figures 41-45 and Tables 7-8*

---

## Part 2. Biogeographic Consideration

In the earlier sections, the ascidians occurring in the Japan Sea and related seas have been scrutinized taxonomically, based on the materials collected newly or treated already in the previous works, as well as through the descriptions presented in the relevant publications. At the same time, the localities of the materials and records were also examined and affirmed for each species. Thus, the biogeographic features of the Japan Sea ascidians can be reexamined on much sounder basis.

The distribution of marine animals in the Japan Sea has been demonstrated biogeographically by many authors, such as Nomura & Hatai (1936), Miyadi, Kuroda & Habe (1953), Utinomi (1955), Horikoshi (1962), Briggs (1974), Okutani & Chinzei (1976), Nishimura (1965a,b, 1966a,b, 1970, 1981), Funahashi (1973), and Yoshizaki & Tanaka (1986). Among them, Nishimura's works were most detailed and extensive, with new intriguing interpretations, and he dealt with almost all kinds of marine animals, of which necessary knowledge was then available. As a consequence, however, the ascidians then poorly known were left little referred to.

Taking into account the results and discussions given in the papers mentioned above, the Japan Sea and adjacent waters are divided into 21 geographic districts for the convenience of analysis of distribution of ascidians, as shown in Fig. 41, and the localities of the ascidians recorded in the present paper are assigned to these districts, yielding the list of the species for each district in Table 7. The districts 1-20 are neritic and include the localities of mediolittoral (indicated as 0 m deep in the present paper only for convenience' sake), infralittoral and circalittoral zones, that is to say, the littoral system. All the ascidian specimens of the present study were not always provided with depth record, and some of them might be collected from deeper zones. However, only a few species have been definitely known to occur exclusively at depths greater than 200 m within the Japan Sea cold water mass (see Ni-

---

1) This is the third and last of serial papers that have been published in this journal as parts of the author's thesis.

2) Present affiliation: Graduate School of Human Informatics.

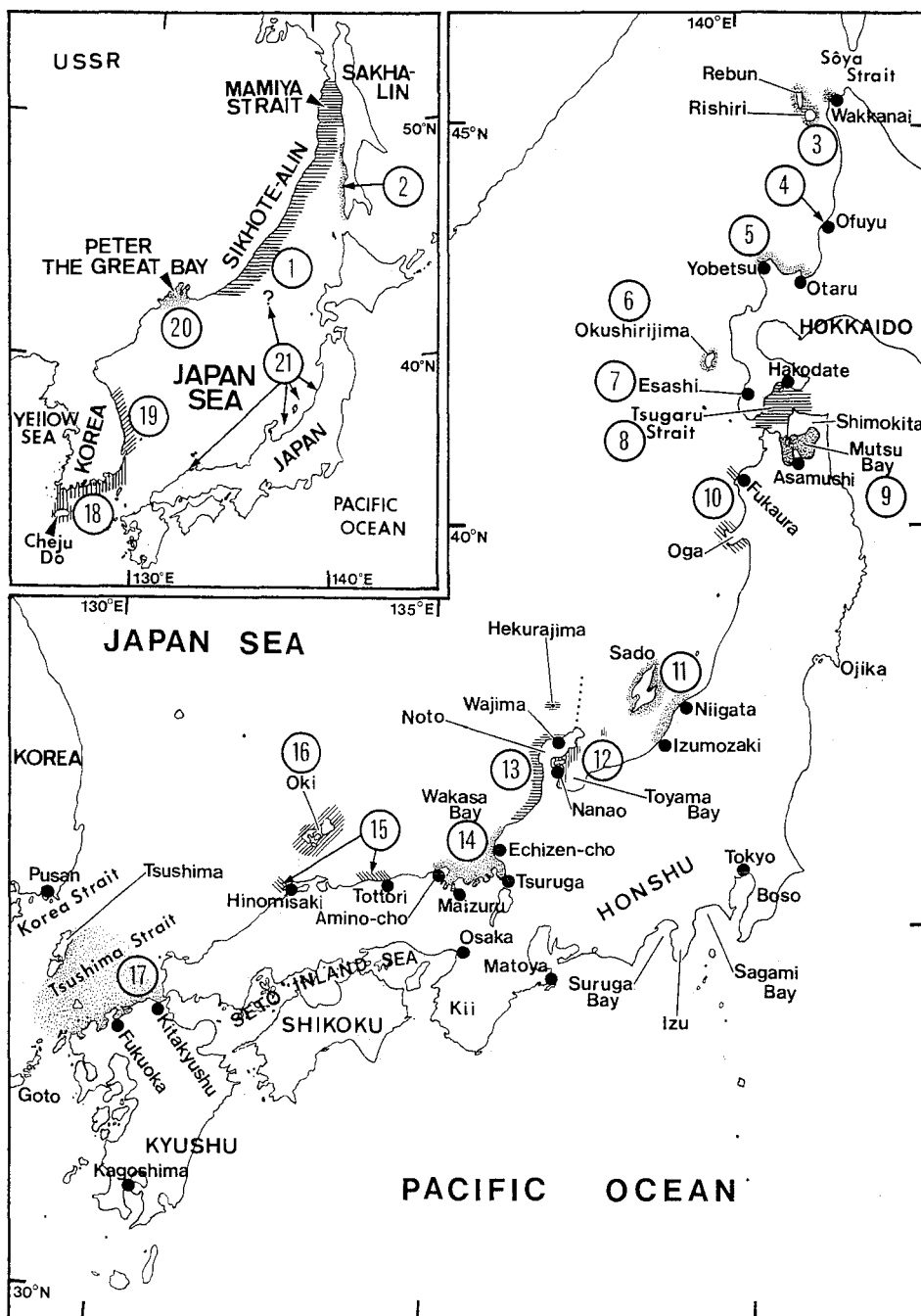


Fig. 41. Map of the continent and island-arc surrounding the Japan Sea, showing localities of shallow-water areas divided into 20 districts (Nos. 1-20) and those of deep-water areas (No. 21).

Table 7. Ascidians recorded so far from the Japan Sea.

Species	District																					Depths (m) recorded in the Japan Sea	Biogeographic distribution type (depths, m, recorded outside the Japan Sea)
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21		
1. <i>Polyclinum saturnium</i> Savigny																		+				?	IWP (4-80)
2. <i>P. sp. aff. saturnium</i> Savigny												+										22-30	JS
3. <i>P. vasculosum</i> Pizon															+							0	WP
4. <i>P. sp. cf. planum</i> (Ritter et Forsyth)														+								shallow	JS
5. <i>Aplidiopsis pannosum</i> (Ritter)															+							0	OB (20-66)
6. <i>Sidneioides japonense</i> Redikorzev															+							0	WP (25)
7. <i>S. snamoti</i> (Oka)																			+			?	JPN
8. <i>Aplidium spitzbergense</i> Hartmeyer		+																				?	ANA (15-415)
9. <i>A. yezoense</i> Tokioka									+													?	JS
10. <i>A. sagamiense</i> (Tokioka)										+	+					+	+					0-6	JPN (0-64)
11. <i>A. multiplicatum</i> Sluiter										+						+		+				0	IWP (0-53)
12. <i>A. rhabdocormi</i> Nishikawa																				+		1380-1410	JPN (300-380)
13. <i>A. constellatum</i> (Verrill)									+													?	?
14. <i>A. pliciferum</i> (Redikorzev)			+		+			+	+		+	+		+				+	+			0-5	WP (1-119)
15. <i>A. glabrum</i> (Verrill)		+			+			+														86-260	ANA (0-366)
16. <i>A. translucidum</i> (Ritter)																				+		?	OB (29-57)
17. <i>A. takii</i> (Tokioka)																	+					85	JS
18. <i>A. ordinatum</i> (Sluiter) sensu Skalkin		+																				?	JS
19. <i>Synoicum clavatum</i> (Oka)																+						3-5	WP (20-100)
20. <i>S. pellucens</i> Redikorzev																				+		30	JS
21. <i>Synoicum sp.</i> sensu Skalkin		+																				?	?
22. <i>Placentela crystallina</i> Redikorzev		+																				?	OB (10-65)

Table 7. (continued)

Species	District																				Depths (m) recorded in the Japan Sea	Biogeographic distribution type (depths, m, recorded outside the Japan Sea)
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	
23. <i>Pseudodistoma antinboja</i> Tokioka																			+		?	JPN (6)
24. <i>Ritterella</i> sp. aff. <i>aequalisiphonis</i> (Ritter et Forsyth)								+													?	JS
25. <i>Didemnum</i> ( <i>D.</i> ) <i>moseleyi</i> (Herdman)					+		+	+	+	+	+	+		+	+	+		+	+	+	?	0-108 IWP (0-400)
26. <i>D.</i> ( <i>D.</i> ) <i>granulatum</i> Tokioka																+						3-5 WP (1-2)
27. <i>D.</i> ( <i>D.</i> ) <i>pardum</i> Tokioka								+		+	+											3-7 JPN (18)
28. <i>D.</i> ( <i>D.</i> ) <i>albidum</i> (Verrill)		+																		+		? ANA (-410)
29. <i>Didemnum</i> ( <i>D.</i> ) sp.			+																			0 JS
30. <i>D.</i> ( <i>D.</i> ) <i>translucidum</i> Tokioka																				+		? JPN (0-150)
31. <i>D.</i> ( <i>D.</i> ) sp. cf. <i>okudai</i> Tokioka									+													? JS
32. <i>D.</i> ( <i>D.</i> ) <i>risirensis</i> Nishikawa			+																			1-6 JS
33. <i>D.</i> ( <i>Polysyncraton</i> ) <i>aspiculatum</i> Tokioka									+			+							+			0-ca. 4 IWP (0-73)
34. <i>Trididemnum savignii</i> (Herdman)											+	+			+	+						0-6 IWA (0-40)
35. <i>T.</i> sp. cf. <i>cerebriforme</i> Hartmeyer									+													15-20 JS
36. <i>T. allenii</i> Berrill sensu Romanov																			+			? JS
37. <i>T. viride</i> (Herdman) sensu Romanov																			+			? JS
38. <i>T. microzoa</i> (Redikorzev)		+																				? JS
39. <i>Leptoclinides madara</i> Tokioka												+	+		+	+		+				0-9 WP (0-5)
40. <i>L. rufus</i> (Sluiter) sensu Romanov																			+			? JS
41. <i>L. komaii</i> Tokioka																+						3-8 JPN (10)
42. <i>L.</i> sp. cf. <i>echinatus</i> Tokioka																+						3-5 JS
43. <i>L. rugosum</i> Tokioka										+												? JS
44. <i>Leptoclinides</i> sp.									+													? ?

Table 7. (continued)

Species	District																					Depths (m) recorded in the Japan Sea	Biogeographic distribution type (depths, m, recorded outside the Japan Sea)
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21		
45. <i>Lissoclinum</i> sp. aff. <i>japonicum</i> Tokioka									+							+						1-20	JS
46. <i>Lissoclinum</i> sp.			+						+													1-7	?
47. <i>Diplosoma mitsukurii</i> Oka					+		+	+	+	+	+	+				+				+	+	0-6	SJ (-60)
48. <i>Clavelina elagans</i> (Oka)																		+				?	JPN (ca.20-99)
49. <i>Eudistoma</i> sp. cf. <i>sagamiana</i> Tokioka					+											+						1-5	JS
50. <i>E. tokiokai</i> Nishikawa											+											?	WP
51. <i>E. illotum</i> (Sluiter)																		+	+			?	?
52. <i>Distaplia dubia</i> (Oka)				+					+	+	+								+	+		0-shallow	JPN
53. <i>D.</i> sp. aff. <i>dubia</i> (Oka) sensu Tokioka											+											?	JS
54. <i>Sycozoa kanzasi</i> (Oka)																+		+				35-45	JPN (92-200)
55. <i>Rhopalaea crassa</i> (Herdman)												+		+		+	+					15-1410	IWP (3-521)
56. <i>Syndia zona grandis</i> Oka														+			+	+				85	SJ (50-ca.100)
57. <i>S. chinensis</i> Tokioka															+							15	WP (30-120)
58. <i>Ciona intestinalis</i> (Linné)									+		+	+		+				+				shallow	COS
59. <i>C. savignyi</i> Herdman									+	+		+		+								0-50	AP
60. <i>Perophora japonica</i> Oka				+					+		+	+	+					+				shallow-81	JPN (-101)
61. <i>P. annectens</i> Ritter																				+		0-10	AP
62. <i>P. sagamiensis</i> Tokioka																+						1-4	WP (0-7)
63. <i>P. multiclathrata</i> (Sluiter)											+											?	IWA
64. <i>Ascidia sydneyensis</i> Stimpson			+		+		+	+	+	+	+	+		+	+	+		+	+			0-55	CT (0-120)
65. <i>A. ahodori</i> Oka									+	+	+	+		+	+							0-30	JPN (0-3)
66. <i>A. gemmata</i> Sluiter									+			+						+				0-100	WP (0-22)

Table 7. (continued)

Species	District																					Depths (m) recorded in the Japan Sea	Biogeographic distribution type (depths, m, recorded outside the Japan Sea)
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21		
67. <i>Ascidia matoya</i> Tokioka														+	+							47-55	JPN (7-10)
68. <i>A. longistriata</i> Hartmeyer											+	+										22-30	JPN (117-350)
69. <i>A. armata</i> Hartmeyer											+	+										100	JPN (-180)
70. <i>A. zyogasima</i> Tokioka																		+				?	JPN (300-450)
71. <i>A. zara</i> Oka			+	+	+		+	+	+	+	+	+		+	+				+	?		0-82	JPN (-140; ?249-366)
72. <i>A. austera</i> Sluiter																+						47-55	WP (0-6)
73. <i>A. callosa</i> Stimpson			+																			?	ANA (0-270)
74. <i>A. sp. aff. obliqua</i> Alder sensu Beniaminson																			+			?	JS
75. <i>Microgastra granosa</i> (Sluiter)								+								+						40-55	WP (0-204)
76. <i>Agnesia himeboja</i> Oka								+			+											5-39	JPN (8-16)
77. <i>A. orthenteron</i> Redikorzev																				+		1900-2090	JS
78. <i>Adagnesia vesiculiphora</i> Nishikawa											+											20	JPN (ca. 45)
79. <i>Rhodossoma turcicum</i> (Savigny)				+				+		+	+	+	+	+	+			+				0-55	CT (0-145)
80. <i>Corella japonica</i> Herdman								+	+	+	+		+	+	+							21-160	IWP (-201)
81. <i>Chelyosoma siboja</i> Oka			+	+	+			+	+					+				+	+			1-52	JS
82. <i>C. dofleini</i> Hartmeyer					+			+														1-20	JPN (183-350)
83. <i>C. yezoense</i> Oka			+	+																		1-4	JPN
84. <i>C. orientale</i> Redikorzev		+																				62-80	OB (18-182)
85. <i>C. macleayanum</i> Broderip et Sowerby		+																				?	ANA (1-565)
86. <i>Chelyosoma</i> sp.							+															1	JS
87. <i>Megalodicopia hians</i> Oka																				+		366	widely (see text)
88. <i>Botryllus primigenus</i> Oka															+			+	+			0	WP

Table 7. (continued)

Species	District																				Depths (m) recorded in the Japan Sea	Biogeographic distribution type (depths, m, recorded outside the Japan Sea)
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	
89. <i>Botryllus tuberatus</i> Ritter et Forsyth		+		+	+	+	+		+	+						+		+	+	+	0-75	CT
90. <i>B. schlosseri</i> (Pallas)		+			+				+	+								+		+	0-15	COS (0-?)
91. <i>B. magnicoecus</i> (Hartmeyer)								+										+			?	IWP (0-15)
92. <i>Botrylloides violaceus</i> Oka			+	+	+	+	+		+		+	+		+							0-8	SJ (0)
93. <i>B. simodensis</i> Saito et Watanabe								+	+	+						+					1-4	WP (0-13)
94. <i>B. lateritium</i> Beniaminson																			+		?	JS
95. <i>B. aureum</i> Sars sensu Skalkin		+																			?	JS
96. <i>Symplegma reptans</i> (Oka)									+					+	+						0-several	SJ
97. <i>S. japonica</i> Tokioka										+	+										0	WP
98. <i>Polyzoa vesiculiphora</i> Tokioka															+						0	JPN
99. <i>P. pacifica</i> Tokioka										+									+		?	JPN
100. <i>Polyndrocarpa</i> (P.) sp. cf. <i>maxima</i> (Sluiter)																+					0	JS
101. <i>Polycarpa cryptocarpa kroboja</i> (Oka)										+	+	+		+	+						1-55	JPN (1-150)
102. <i>P. doederleini</i> Hartmeyer												+				+	+	+			30-55	JPN
103. <i>P. aurita</i> (Sluiter)																+					35-55	IWP (2-38)
104. <i>P. maculata</i> Hartmeyer										+		+		+		+	+	+			35-118	WP (0-200)
105. <i>P. psammotesta</i> Tokioka								+						+							110	JPN (100-400)
106. <i>P. granosa</i> Tokioka														+							?	JPN (0)
107. <i>P. divisa</i> (Ostroumov et Pablenko)																			+		45-84	OB (100)
108. <i>Cnemidocarpa irene</i> (Hartmeyer)								+	+	+	+	+	+	+	+	+	+	+	+		0-55	IWP (0-130)
109. <i>C. clara</i> (Hartmeyer)		+	?	+		+	+	+	+			+		+	+			+	+	+	1-115	AP (0-140)
110a. <i>C. fertilis fertilis</i> (Hartmeyer)											+							+			105-117	JPN (20-400)



Table 7. (continued)

Species	District																					Depths (m) recorded in the Japan Sea	Biogeographic distribution type (depths, m, recorded outside the Japan Sea)
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21		
110b. <i>Chemidocarpa fertilis minor</i> Tokioka										+				+		+						30-62	JPN (-549)
111. <i>C. miyadaii</i> Tokioka			+	?										+			+					ca. 25	JPN (8-10)
112. <i>C. ramosa</i> Nishikawa												+										22-30	JS
113. <i>C. sp. cf. javensis</i> Millar																+						30-35	JS
114. <i>Styela plicata</i> (Lesueur)									+		+		+									1-25	COS (-80)
115. <i>S. canopus</i> Savigny										+	+	+		+	+			+				0-40	CT (0-?)
116a. <i>S. clava clava</i> Herdman			+	+	+		+	+	+	+	+			+				+	+	+		1-ca. 70	OB
116b. <i>S. clava symmetrica</i> Tokioka										+	+	+						+				21-81	JPN (18)
117. <i>S. longipedata</i> Tokioka														+								?	JPN (-92)
118a. <i>S. coriacea coriacea</i> (Alder et Hancock)		+			+				+	+	+					+				+		-81	ANA (-662)
118b. <i>S. coriacea hemicaespitosa</i> Ritter												+										45	OB (33-412)
119. <i>S. rustica</i> (Linné)	+	+																				14-30	ANA (0-432)
120. <i>S. monogamica</i> Oka									+													?	JS
121. <i>S. sigma</i> Hartmeyer											+											?	? (60-450)
122. <i>S. tokiokai</i> Nishikawa									+		+		+					+	+			1-10	JPN
123. <i>Dendrodoa aggregata</i> (Rathke)	+	+							+									+	+	+		3-110	ANA (0-707)
124. <i>D. pulchella</i> (Verrill)	+																					64	ANA
125a. <i>Peloniaia corrugata corrugata</i> Goodsir et Forbes	+																			+		0-200	ANA (4-200)
125b. <i>P. corrugata bursaria</i> Redikorzev	+	+																		+		4-900	OB (503-1366)
126. <i>Pyura vittata</i> (Stimpson)			+	+	+	+	+		+	+	+		+	+	+		+					0-55	SJ
127. <i>P. saciformis</i> (Drasche)						+			+	+	+		+	+	+		+	+				1-110	JPN (0-90)
128. <i>P. lepidoderma</i> Tokioka			+						+		+		+	+	+		+					1-1410	WP (-119)

Table 7. (continued)

Species	District																					Depths (m) recorded in the Japan Sea	Biogeographic distribution type (depths, m, recorded outside the Japan Sea)
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21		
129. <i>Pyura</i> sp. cf. <i>lignosa</i> Michaelsen									+	+		+		+	+	+						0-81	WP (5-13)
130. <i>Herdmania momus</i> (Savigny)												+		+	+	+		+				0-55	CT
131. <i>H. mirabilis</i> (Drasche)					+			+						+				+	+			3-20	AP (0-60)
132a. <i>Bolteria echinata echinata</i> (Linné)	+	+	?															+		+		55-200	ANA (0-297)
132b. <i>B. echinata iburi</i> (Oka)	+	?		+	+	+		+	+	+		+		+	+	+		+	+			0-100	AP (-200)
133. <i>B. transversaria</i> (Sluiter)																	+					30-45	IWP (0-18)
134. <i>B. ovifera</i> (Linné)			+																			?	ANA (73-494)
135. <i>Halocynthia aurantium aurantium</i> (Pallas)	+	+	+		+														+	+		1-100	OB
136. <i>H. roretzi</i> (Drasche)	+		+		+	+	+	+	+	+	+	+		+		+		+	+	+		0-62	SJ (0-64)
137. <i>H. hispida</i> (Herdman)					+			+	+	+	+	+	+	+		+		+	+			1-1410	IWP (0-676)
138. <i>H. igaguri</i> Tokioka																+						35-55	JPN (-12)
139. <i>H. turboja</i> (Oka)												+	+	+								74-1410	JPN (108-183)
140. <i>Microcosmus hartmeyeri</i> Oka												+		+		+						1-55	WP (1-150)
141. <i>M. multitentaculatus</i> Tokioka										+		+	+	+				+				10-1410	JPN
142. <i>Hartmeyeria orientalis</i> Oka			+	?								+					+					?	JPN (25-80)
143. <i>H. triangularis</i> Ritter	+																					22	OB (17-22)
144. <i>Eugyra glutinans</i> (Moeller)	+							+	+		+									+		3-108	ANA (6-1805)
145. <i>E. communis</i> Nishikawa										+				+								45-59	JS
146. <i>E. extrorsa</i> Nishikawa										+												29-32	JS
147. <i>Pareugyrioides japonica</i> (Oka)								+		+												45-59	JS
148. <i>P. dalli</i> (Ritter)																				+		15-200	OB (9-100)
149. <i>Molgula xenophora</i> Oka								+	?		+						+	+				63-118	JPN (92-400)



Table 8. Number of littoral and eurybathic ascidian species of the Japan Sea for each district and for each type of biogeographic distribution.

Biogeographic distribution type	District																				Total
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	
WP	0	0	2	0	1	0	1	3	4	4	3	8	1	5	6	11	1	6	2	0	20
IWP	0	0	0	0	2	0	1	4	5	3	2	5	1	4	2	6	2	5	2	1	10
IWA	0	0	0	0	0	0	0	1	0	1	3	2	1	1	2	2	1	1	1	0	3
CT	0	1	1	1	3	1	2	1	3	2	3	4	0	4	4	4	0	4	3	1	5
EA: SJ	1	0	3	2	4	3	4	2	5	3	3	4	0	5	2	3	1	3	1	2	6
EA: JPN	0	2	2	0	5	1	2	3	10	11	11	17	3	14	5	10	4	14	5	1	42
EA: JS	1	2	3	1	2	0	1	3	6	4	1	2	0	3	0	5	1	1	1	6	32
AP	2	0	2	1	3	1	0	2	4	2	0	3	0	4	2	1	0	3	3	2	5
OB	5	4	2	1	2	0	1	1	1	1	1	1	0	1	1	0	0	1	2	7	13
ANA	8	10	0	0	2	0	0	1	3	2	0	2	0	0	0	1	0	2	1	6	14
COS	0	1	0	0	1	0	0	0	3	0	1	2	0	2	0	0	0	2	0	1	3
Uncertain	0	1	1	0	0	0	0	1	2	0	1	0	0	0	0	0	0	1	1	0	7
Total	17	21	16	6	25	6	12	22	46	33	29	50	6	43	24	43	10	43	22	27	160

shimura, 1982a, p. 382), and these deep-sea ascidians are the members of the district 21.

In Table 7, the pattern of biogeographic distribution each species shows is also designated, following mainly the system of Nishimura (1971, pp. 170–179; 1981, pp. 216–241). The biogeographic distribution codes used stand for as follows.

WP: West Pacific

IWP: Indo-West Pacific

IWA: Indo-West Pacific & tropical-warm temperate Atlantic

CT: circum-tropical

SJ: Sino-Japanese

JPN: Japanese

JS: Japan Sea

AP: amphi-Pacific

OB: Okhotsk-Bering

ANA: Arctic-North Atlantic

COS: cosmopolitan

SJ, JPN and JS represent subtypes of the east Asiatic endemic (EA) type of distribution. WP type of occurrence is distinguished in the present analysis provisionally from IWP type to emphasize that some species are known only from the West Pacific, and not from the Indian Ocean. This assignment is, of course, rather tentative in the sense that the world-wide reliable information of distribution and taxonomy of the ascidians is still wanting.

Of the 163 ascidians (including several of infraspecific rank) recorded from the Japan Sea, 160 are shallow-water (littoral or eurybathic) and only 3 are deep-water species. Table 8 shows the numbers of littoral and eurybathic species in each district

for each type of biogeographic distribution. Altogether, the shallow-water species consist of 80 (50%) east Asiatic (including 32 endemic to the Japan Sea), 38 (24%) warm-water (i.e. WP+IWP+IWA+CT), 32 (20%) cold-water (i.e. AP+OB+ANA), 3 (2%) cosmopolitan, and 7 (4%) unattributable species. The deep-water species include 1 endemic to the Japan Sea, 1 endemic to the vicinity of Japan, and 1 species distributed widely. The remarkably high proportion of east Asiatic endemic species is noteworthy. Different numbers of species among 20 neritic districts seem to be largely due to difference in collecting effort so far paid, and it should be noted that in districts 4, 6, 7, 13 and 17 only a few collections are available.

According to Nishimura's (1981, pp. 242-243) recognition, some of the distributional types are attributable to either the northern or the southern group; AP, OB and ANA are the elements of the northern group, and WP, IWP, IWA and CT are of the southern. The species of EA type, that are assumed to be derived from an extraneous mother species, judging from distributions of their related species and/or genera, are also regarded to be attributable to either group. Thus, in this sense, *Chelyosoma siboya*, *C. dofleini*, *C. yezoense*, *C. sp.*, *Ascidia zara*, *Cnemidocarpa fertilis fertilis*, *C. fertilis minor*, *C. miyadaii* and *Styela clava symmetrica* are elements of the northern group, while *Sidneioides sunamoti*, *Pseudodistoma antinboja*, *Sycozoa kanzasi*, *Polyandrocarpa (P.) sp. cf. maxima*, *Polycarpa cryptocarpa kroboja* and *P. doederleini* the southern group. In Fig. 42, the species compositions of the reported ascidians in the respective districts (except district 21) are illustrated in terms of the groups.

On the basis of these treatments and premises, some particular considerations

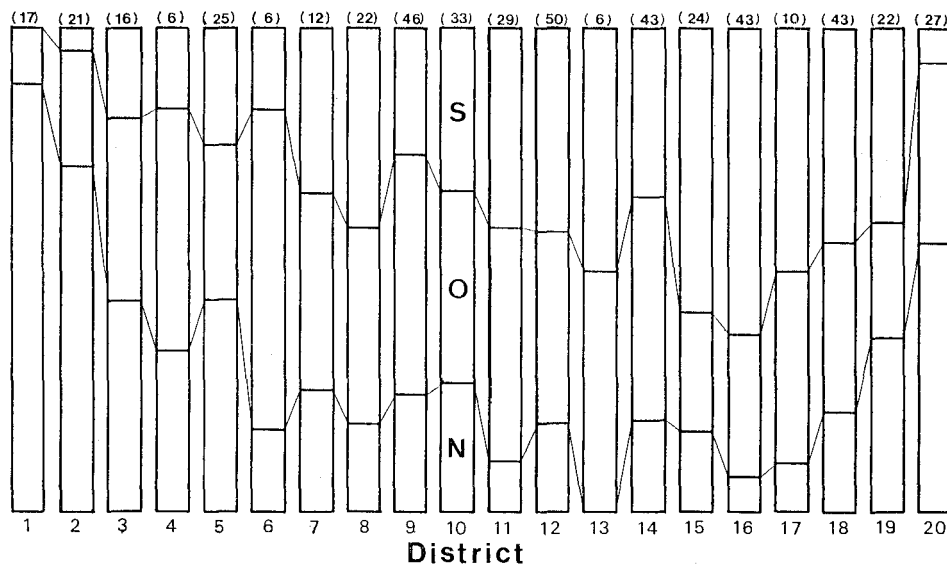


Fig. 42. Composition of shallow-water ascidians in each district, expressed as the proportion of numbers of species of three groups. N and S indicate northern and southern groups (for definition see the text) respectively, and O the group of species not assignable to either group. Number of species recorded in each district is indicated in parentheses above each column.

will be presented on the biogeography of the Japan Sea ascidians in the following.

(A) Distribution of ascidians within the Japan Sea

The limit of local bathymetric (vertical) distribution for shallow-water species in the Japan Sea, especially along the Japanese coasts, is expected to be influenced by the existent thickness of the Tsushima Current flowing into there (see Nishimura, 1981, pp. 243–247). However, the lack of record of the depth of collection in many of present ascidian specimens makes it inadequate to extend the analysis on this subject. Geographic (horizontal) distribution is, thus, examined for littoral and eurybathic species, and deep-water species are treated in other section.

As shown in Fig. 42, relatively great difference in species composition between contiguous districts is noticeable at several particular sites; namely between 1 and 20, 2 and 3, and 19 and 20, and less markedly between 1 and 2, 5 and 6, 17 and 18, and 18 and 19. On the other hand, between districts 3 through 5, the species composition remains virtually unchanged. With higher latitude from district 6 through district 17 (except 9 and 14), the percentage of the species of the southern group decreases nearly gradually, while that of the northern group remains almost constant. The highest percentage of southern elements and the lowest of northern elements are both found in district 16 encompassing Oki Islands. Relative scarcity of southern elements in district 17 of Tsushima Strait at the southern entrance to the Japan Sea appears strange, but this may be resulted from the scanty collection there. On the contrary, the scarcity of southern elements in district 9 of Mutsu Bay and in district 14 of Wakasa Bay, as compared to their neighboring districts (except district 13 with only 6 species recorded), is regarded to be reliable, because these districts have been relatively well investigated.

The range or extent of occurrence of each species is shown in Fig. 43. Prominent successive disappearance of the southern species towards the north is illustrated concordantly on both the continental and the Japanese coasts, with no southern species in the northern-most district 1. On the other hand, many northern species are absent southerly beyond the Sakhalin coast (district 2), and the rest disappear more or less gradually, though rather markedly in districts 12 to 16, along the Japanese coast, with only a single species attaining Tsushima Strait (district 17). On the continental coast, however, although some northern species show their southern limit at Peter the Great Bay (district 20), others occur further south on the Korean shore facing Korea Strait (district 18), more southerly than along the Japanese coast. Marked disappearance of some species is noticed between several adjacent districts; namely between districts 11 and 12, 15 and 16, and 18 and 19 in the southern group, while between districts 1 and 2, 2 and 3, 1 and 20, 17 and 18, and 19 and 20 in the northern group. Among the species of the southern group, *Botryllus tuberatus* (regarded as CT) is distributed most northerly, followed by *Ascidia sydneyensis* (CT) and *Aplidium pliciferum* (WP). The EA elements of this group disappear far more southerly than expected by Nishimura (1981, p. 247; and elsewhere). According to him, the EA species of the southern group are found more northerly than any other elements of the group in various kinds of animals. This conclusion is drawn from his

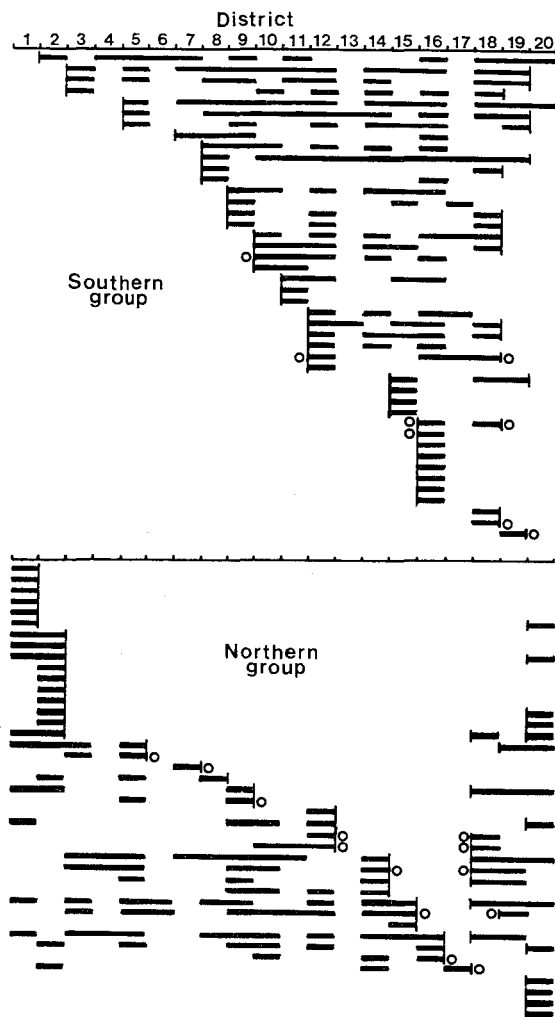


Fig. 43. Occurrence of respective species ascribed to the southern (top) or northern (bottom) groups. Horizontal bars indicate the occurrence of a species in the district concerned; the bars in a level are for the same species. Vertical short line touching one end of bars means the termination of range within the Japan Sea. Open circles represent the EA species regarded obviously as having derived from the warm-water (in the southern group) or cold-water (in the northern one) mother species.

speculations on the origin of the EA species, and the inconsistency of the present result to this is not understood. In contrast, the EA species of the northern group are the major components of the ascidians of this group distributed far south, as clearly shown in the figure, as can be expected from Nishimura's (1981, pp. 235-236) supposition.

Distribution patterns of northern and southern species shown in the these two figures agree with the supposition by Nishimura (1965a, p. 51), which leads him to divide the Japan Sea into "the southeastern warm-water area washed by the Tsushi-

ma Current and the northwestern cold-water area under the influence of the Liman Current" (Nishimura, 1982a, p. 382). The far greater penetration of northern species into Korea Strait than Tsushima Strait conforms very well to that. Yamada (1933) previously claimed that the surface water (less than 50 m deep) of Korea Strait is almost devoid of "temperate oceanic plankton" (p. 281), while richly inhabited by neritic species, and is distinguishable by these features clearly from that of Tsushima Strait. He suggests that Korea Strait is influenced predominantly by cool neritic water along the continent, but seldom by the warm Tsushima Current. According to Tsukuda's (1937) Plate XIII, the water along the Korean coast facing Korea Strait is cooler by about 4°C in annual mean surface temperature than that along the corresponding Japanese coast.

Surprisingly low percentage of southern species in districts 9 (Mutsu Bay) and 14 (Wakasa Bay) (Fig. 42) may be related to the relative coolness of water in these districts, as suggested for the fish fauna of Mutsu Bay by Shiogaki (1985) and as shown by plankton investigations of Wakasa Bay by Asaoka & Furuhashi (1985, p. 974). Low temperature cannot fully explain why these districts are rich in COS species, as shown by "O" in Fig. 42, rather than northern ones.

(B) Comparisons of the ascidian fauna among the Japan Sea and several other regions

(B1) Overall estimate of the richness

Tokioka (1963) listed 302 ascidians (including the taxa of infraspecific rank) from Japanese and adjacent waters inclusive of "the Okhotsk Sea, the Japan Sea and the waters surrounding Tisima (the Kurile Islands), Karahuto (Sakhalin), four main islands of Japan, the Okinawa Islands, Ogasawara (the Bonin Islands), Formosa and Korea." Since then, many taxonomic contributions have been made to the ascidian fauna of these regions, resulting in the addition of many newly recorded species and the deletion of some species names through taxonomic revision. At present, the fauna includes roughly 340 species of ascidians. Of these, 163 are known from the Japan Sea, amounting to about half of the whole.

To evaluate the specific diversity, the ascidian fauna of the Japan Sea is compared with that of another enclosed sea, the Mediterranean. Since the publication of an early estimate of 132 ascidian species by Pérès (1967, tab. 1), much has been added to the knowledge of the Mediterranean ascidian fauna. According to C. Monniot, being read from his data bank 'MEDIFAUNA', 201 species are presently known from the Mediterranean, that include 40 uncertain or doubtful ones. Of these 201 species, 9 are found at depths greater than 200 m. The larger number of deep-sea ascidians found in the Mediterranean Sea than in the Japan Sea (3 species) is a consistent trend to the overall poverty of the deep-water fauna in the Japan Sea ascribed to the particular features of the "Japan Sea cold water mass" filling the basin (see Nishimura, 1974, pp. 166–177; also Section (C) below). Or, it may be attributable to far more effort of sampling done in the Mediterranean. According to Briggs (1974, pp. 203–206), the greater richness of the Mediterranean fauna compared to that of the Atlantic coast may be due to very high endemism in the Mediterranean; Pérès



(1967) estimated that 50.4% of the 132 species are endemic, while Monniot listed 101 (50.2%) of the 201 species to be known exclusively from the Mediterranean Sea. Compared with these figures, the percentage of endemic species in the Japan Sea is far lower (only about 20%). However, about half of 163 ascidian species of the Japan Sea are the east Asiatic endemic element (inclusive of the Japan Sea endemic ones).

Comparison of ascidian fauna between the Japan Sea and the Pacific coasts of Japan demonstrates some characteristics of species diversity in the Japan Sea. Kii Peninsula, situated on the Pacific coast of the middle Honshu and influenced by the Kuroshio Current, is taken as a representative of the Pacific coast, and 113 ascidian species have been reported from its waters. This number is nearly equal to that of ascidian species found collectively in districts 9 through 16, covering nearly the whole Japan Sea coast of Honshu (see Fig. 41). The result is reminiscent of the general statement that the Japan Sea coast of Honshu is extremely poor in both variety and number of littoral or coastal organisms as compared with the Pacific coast of the southern Japan, especially on the rocky shore (see, for example, Nishimura, 1970; Saito, 1970).

To examine this view on the variety of rocky-shore ascidians, a brief comparison is made for ascidian materials collected by myself from Oki Islands in the Japan Sea and from Kii Peninsula, using the same collecting method (mainly by snorkelling) and with similar collecting effort. The materials from Oki Islands (C-8 in the present study) collected in August 1981 at 9 sites, include 23 species (14 warm-water, 8 EA and 1 cold-water), and those from Kii Peninsula (A-6, 7, 9 (part) to 12 and 14 to 16 in Nishikawa (1980b)), collected in July-August 1979 at 9 sites, consist of 32 species (21 warm-water, 9 EA, 1 cold-water and 1 COS). This difference in species number and composition is clearly due to the scarcity of warm-water species in the Oki Islands area. Thus, the paucity of ascidian fauna in the Japan Sea should be discussed first with reference to its warm-water species.

#### (B2) Warm-water ascidians

Warm-water species are believed to be conveyed or recruited from the tropical southeast Asiatic seas northerly to the waters of Japan by the dominating Kuroshio Current, and some are transported into the Japan Sea by the Tsushima Current which originates in the Kuroshio west of Kyushu, being mixed with the low-salinity surface water of the East China Sea (Nishimura, 1982a, p. 380; Nagata, 1987, p. 95). To estimate the contribution of the Tsushima Current to the ascidian fauna of the Japan Sea, this fauna is compared with that of the tropical coastal waters of the Nansei Archipelago, though the ascidian fauna of this archipelago has not been well studied. Of approximately 52 species so far recorded from the archipelago (Tokioka, 1954a; Tokioka & Nishikawa, 1975; Nishikawa & Tokioka, 1976a,b; Nishikawa, 1987), only 16 species (about 30%) are known also from the Japan Sea, while 26 occur on the Pacific coast of Honshu. Of course, there are many warm-water species that have not yet been recorded from the archipelago, but have been recorded from the Japan Sea and the Pacific coast of Honshu. Even if this situation is considered, these figures show clearly that the majority of the ascidians found in the Nan-

sei Archipelago cannot enter into the fauna of the Japan Sea, aided by the Tsushima Current, while some more species are carried over to the Pacific coast of Honshu by the Kuroshio proper. In this context, however, the claim made by Nishimura (1970; and also elsewhere) must be also taken into account that some tropical species coming all the way into the Japan Sea may fail to settle down there under its unfavorable hydrographical conditions such as dilution of surface water in summer and marked lowering of mean sea level in winter. It remains unknown to which ascidians the claim may be applicable, but here it may be just enough to remember Millar's (1971) view that "ascidians in general are animals of rather high salinity water" and "low salinity may preclude breeding owing to the sensitivity of the zygotes, embryos or larvae, while permitting the maintenance of the more tolerant adults."

The littoral ascidian fauna of Kii Peninsula has been well studied; according to Nishikawa (1988), there are 113 ascidian species, comprising 32 species regarded as WP element, 9 as IWP, 5 as IWA, 5 as CT, 6 as SJ, 40 as JPN, 3 as AP, 1 as OB, 2 as ANA and 3 as COS, besides other 7 species of uncertain derivation; thus the warm-water species ( $=WP+IWP+IWA+CT$ ) occupying 45% (51 species) of the fauna, the endemic ones ( $=SJ+JPN+JS$ ) 41% (46 species) and the cold-water forms ( $=AP+OB+ANA$ ) only 5% (6 species). Its ascidian fauna is characterized by the high percentage of warm-water species and the extreme scarcity of cold-water forms, as compared with the Japan Sea. Of 113 species found around Kii Peninsula, 68 species also occur in the Japan Sea, and they include 15 WP, 8 IWP, 3 IWA, 5 CT, 5 SJ, 23 JPN, 3 AP, 1 OB, 2 ANA, and 3 COS species. Of these species, the cold-water CT and COS species are fully represented and the IWP, IWA and SJ ones are nearly so, while only half of the WP species recorded from the Kii Peninsula region are shared with the Japan Sea. Of the 38 warm-water species occurring in the Japan Sea, 7 are not known from the Kii Peninsula region, which include 5 WP and 2 IWP species. Taking all these figures into consideration, the difference in number of warm-water species between the Japan Sea and the Kii Peninsula region may be attributable largely to the scarcity of WP species in the Japan Sea. In other words, WP species generally seem to inhabit the Japan Sea far more rarely than IWP, IWA or CT ones do; this might support to introduce the distinction of WP from IWP. The IWP, IWA and CT species have each a wider geographical distribution than the WP species, suggesting their greater adaptability to varied habitats. Indeed, for instance, *Aplidium multiplicatum* (of IWP), *Perophora multiclathrata* (IWA), *Botryllus magnicoecus* (IWP) and *Herdmania momus* (CT) are abundant on more or less exposed coral reef areas in the West Pacific (Nishikawa, 1984a, 1986a), but also inhabit more or less protected areas in Japanese waters. Another IWP ascidian *Polycarpa aurita* inhabiting mainly coral reef areas is dredged around Oki Islands in the Japan Sea, though not yet recorded from the Pacific coast of Honshu; this species is known also from the pearl-oyster bed in the Arafura Sea. Some WP ascidians show as great adaptability as the above-mentioned IWP, IWA or CT species; for example, *Aplidium pliciferum* is found on more or less exposed coral reefs in low latitudes, but also flourishes in embayments on both the Japan Sea and Pacific coasts of Japan.

The poorness of WP species in the Japan Sea may also be interpreted from the previous observation "that many...animals inhabiting the tropical-subtropical rocky or coral reefs and commonly observed on the exposed shores on the Pacific side of the southern and central Honshu are quite poor or missing altogether in the Japan Sea" (Nishimura, 1966a, p. 376), owing to the above-mentioned unfavorable hydrographic conditions of the sea. Such animals are termed "high-salinity shelf species" (Nishimura, 1982a, p. 384). Of the 15 WP ascidians occurring in Kii Peninsula waters but absent from the Japan Sea, at least the following 7 species may be categorized as such: *Polyclinum sundaicum* (= *P. tsutsuii*), *Aplidium yamazii*, *Clavelina viola*, *Polycitor proliferus*, *Polyandrocarpa* (*Eusynstyela*) *misakiensis*, *Polycarpa pedata* and *Pyura curvigna*. On the other hand, some WP ascidians found abundantly on more or less exposed coral reefs in low latitudes also occur in the Japan Sea. Such ascidians are exceptions to Nishimura's generalization. They are *Perophora sagamiensis* and *Polycarpa maculata*. The former is found very rarely in the Japan Sea with mature gonads, and therefore is considered to occur there as a pseudopopulation. On the contrary, the latter seems to thrive there. *Polycarpa maculata* is found commonly in the medio- to infralittoral zones (mostly up to 14 m), attached firmly to the reef corals or their dead fragments in the West Pacific inclusive of the Nansei Archipelago. It has been dredged from the sandy floor at depths of 30 m or more off the Pacific coast of Honshu and the Japan Sea, as well as the Tasmanian coast (see the descriptive section). Almost the same is the case with an IWP ascidian *Corella japonica*, though it has not been recorded from Tasmanian waters. Significant difference in recorded depth cannot be explained.

It should be mentioned, with respect to Nishimura's generalization, that there are 7 warm-water species which have been recorded very rarely from the Japan Sea but have never been from the Kii Peninsula region. They are *Polyclinum vasculosum* (WP), *Sidneioides japonense* (WP), *Ascidia austera* (WP), *Microgastra granosa* (WP), *Polycarpa aurita* (IWP), *Boltenia transversaria* (IWP) and *Molgula celebensis* (WP) (see Table 7). Although sufficient information on their habitat and occurrence in low latitudes is still wanting, fragmental records suggest that at least *A. austera* is possibly a "high-salinity shelf species." If so, this may present another exception to Nishimura's view. Despite its extremely sporadic occurrence in the Japan Sea, the only specimen so far collected and examined has mature gonad. This case reminds me of the occurrence of a barnacle on the shores of Oga Peninsula and Noto Peninsula in the Japan Sea, that resembles closely the warm-water mediolittoral *Tetraclita formosana* Hiro, 1939 (Yajima, 1978, p. 27). *T. formosana* has been recorded exclusively from Formosa and the Pacific coasts of Japan from Iriomote Island of the Nansei Archipelago northerly to Izu Peninsula of south central Honshu and Amakusa of west Kyushu, inhabiting the exposed rocky shores directly washed by the oceanic water (Yamaguchi, 1986). Although this species is clearly an EA element, not WP, its habitat indicates it to be categorized as a "high-salinity shelf species." If that unidentified barnacle be *T. formosana*, the occurrence of species of this category in the Japan Sea is undeniable.

The species of EA type of geographic distribution have been argued of their origin and are assumed likely to have diverged and differentiated in waters of more or less embayment situation. If they expanded their range into new areas of similar conditions, and if they found the requisite conditions in the Japan Sea (indeed, the Japan Sea itself is urged to be embayment-like in its diluted summer surface water), they might have invaded into there.

(B3) Semi-enclosed sea ascidians

The littoral fauna of the Japanese coast of the Japan Sea has been indicated to be dominated by embayment organisms (see, for example, Nishimura, 1970; Okiyama, 1974; Horikoshi, 1976). For comparison, Osaka Bay and the Seto Inland Sea of west Honshu and Ariake Sea of west Kyushu are selected, where ascidian fauna has been studied comparatively well. Of the 38 species recorded from Osaka Bay by Hartmeyer (1906) and Tokioka (1951b, 1954d, 1962b), that were subsequently revised by me, 29 species (76%) are shared with the Japan Sea; the 38 species contain 3 WP, 3 IWP, 1 IWA, 3 CT, 4 SJ, 10 JPN (including 2 not known from the Japan Sea), 3 AP, 1 OB, 1 ANA and 3 COS, as well as 5 endemic to the bay and 1 species of uncertain type. Of the 24 species so far known from the Seto Inland Sea by Tokioka (1953a), Tokioka & Kado (1972) and my own research and revision, comprising 1 WP, 1 IWP, 1 IWA, 3 CT, 2 SJ, 8 JPN, 3 AP, 1 OB, 1 ANA, 2 COS and 1 endemic species, 21 (88%) are recorded also from the Japan Sea; 1 JPN species (*Symplegma connectens* Tokioka) and 1 COS species (*Molgula manhattensis* (De Kay)) are not yet recorded from the Japan Sea. Among the 13 species reported from Ariake Sea by Tokioka (1960b), consisting of 1 WP, 1 IWP, 2 CT, 1 SJ, 3 JPN, 1 AP, 1 COS, 1 endemic and 2 species of uncertain type, 10 (78%) are known also from the Japan Sea. These figures show that many of the species inhabiting semi-enclosed sea areas or embayments are included in the ascidian fauna of the Japan Sea.

Among the species common to the Japan Sea and the semi-enclosed seas on the Pacific side, *Halocynthia igaguri* is endemic to the Japan Sea and the Seto Inland Sea, and *Microcosmus multitentaculatus* has been found exclusively in the Japan Sea, the Seto Inland Sea and Ariake Sea, especially abundantly in the Japan Sea. In the Japan Sea, however, these two species inhabit both protected and exposed areas. In the exposed areas of the Japan Sea, *H. igaguri* occurs at depths of 35–55 m and *M. multitentaculatus* at 10–110 m, while in the semi-enclosed seas of the Pacific side, *H. igaguri* ranges only down to 12 m and bathymetric data are not available for *M. multitentaculatus*. *Ascidia matoya* and *Molgula oligostriata* have been recorded on the Pacific coast only from the protected bottom of Matoya Bay (at 7–10 m and 12 m respectively), while on the Japan Sea coast they are found from more or less exposed floors at depths of 47–55 m and 29–42 m respectively. Why these species occur in the Japan Sea in the exposed areas at deeper depths than in semi-enclosed seas of the Pacific side can be explained in view of the fact that “during the summer the entire Japan Sea is covered with a surface community dominated by embayment or neritic organisms” (Nishimura, 1982a, p. 384; for many examples see also Nishimura, 1965a, pp. 57–65; 1965b, pp. 87–88; and elsewhere), showing that neritic water

develops much more extensively in the Japan Sea than along the Pacific coast. The distribution of *Perophora japonica*, occurring in both protected and exposed areas in the Japan Sea and in exposed areas on the Pacific side, appears apparently incompatible with this situation. Complete absence of *Molgula manhattensis* from the Japan Sea seems also strange, because it has been invading the bottom or inner area of many embayments on the Pacific coast of Japan (see Nakauchi & Kajihara, 1981) since 1972 when it was first found in Japan in the waters of Takehara City in the Seto Inland Sea (see Tokioka & Kado, 1972). The absence of this ascidian should be contrasted with the successful colonization by *Mytilus edulis galloprovincialis* Lamarck, 1819, *Balamus eburneus* Gould, 1841 and *B. improvisus* Darwin, 1854 throughout the Japan Sea coast of Honshu since 1950–1960's, in contrast to their distributions on the Pacific coast seemingly restricted to more or less highly protected or low-salinity areas (see Nishimura, 1970, p. 36); these along with *M. manhattensis* are regarded as fouling animals (Arakawa, 1980).

Lastly, brief references are made to the ascidians inhabiting the embayments in Japanese waters. Ecological or quantitative studies of the ascidians are almost lacking, and the following is a preliminary list of the ascidians commonly, though not exclusively, found on soft bottoms and/or rocky shores in the embayments of the Pacific coast of southern Japan, with their biogeographic distribution type designation in parentheses: *Aplidium sagamiense* (JPN), *A. multiplicatum* (IWP), *A. pliciferum* (WP), *A. yamazii* (JPN), *Didemnum* (*Didemnum*) *moseleyi* (IWP), *Trididemnum savignii* (IWA), *Leptoclinides madara* (WP), *Diplosoma mitsukurii* (SJ), *Distaplia dubia* (JPN), *\*Ciona intestinalis* (COS), *\*C. savignyi* (AP), *Ascidia sydneyensis* (CT), *A. ahodori* (JPN), *A. zara* (JPN), *Agnesia himeboja* (JPN), *Rhodosoma turcicum* (CT), *Corella japonica* (IWP), *Botryllus tuberatus* (CT), *B. schlosseri* (COS), *Botrylloides violaceus* (SJ), *B. simodensis* (WP), *Symplegma reptans* (SJ), *Polycarpa doederleini* (JPN), *Cnemidocarpa irene* (IWA), *C. clara* (AP), *\*Styela plicata* (COS), *S. canopus* (CT), *S. clava clava* (OB), *Pyura vittata* (SJ), *P. saciformis* (JPN), *P. lepidoderma* (WP), *Boltenia echinata iburi* (AP), *Halocynthia hispida* (IWP), *Microcosmus multitentaculatus* (JPN), *Hartmeyera orientalis* (JPN), *Eugyra glutinans* (ANA), and *\*Molgula manhattensis* (COS). The species marked with an asterisk are found even in the inner-most part of the embayments, so far as I am aware, while many others may be of low embayment degree (see Miyadi & Masui, 1942a, p. 113; 1942b, p. 9; Horikoshi, 1976, pp. 219 & 221). Of these 37 species, 14 (38%) are warm-water species, 14 (38%) east Asiatic endemic (4 SJ and 10 JPN), 5 (13%) cold-water, and 4 (11%) cosmopolitan. The endemic species apparently form a large, but not predominant, part of the embayment ascidian fauna. This brings to mind several authors' statements that the littoral areas, especially embayments, around the Japanese islands are inhabited by many species endemic to the Japanese and adjacent waters (Okutani & Chinzei, 1976; Nishimura, 1981), and such species are categorized as a "continental-coast element" (Miyadi, Kuroda & Habe, 1953) or "Japanese element" (Horikoshi, 1962).

#### (C) Deep-water ascidian fauna of the Japan Sea

The deep-water ascidian fauna has hitherto been investigated insufficiently in

the Japan Sea. Only a single reliable record is available for St. 21 of collection A of the present study, located in Toyama Bay at a depth of 1380–1410 m. The fauna consists of *Aplidium rhabdocormi* (one of the deep-water species defined elsewhere), *Rhopalaea crassa* (an IWP element), *Pyura lepidoderma* (WP), *Halocynthia hispida* (IWP), *H. turboja* (JPN) and *Microcosmus multitentaculatus* (JPN). All these species, except *A. rhabdocormi*, show high eurybathy in the Japan Sea; *R. crassa* and *H. hispida* are eurybathic also outside the Japan Sea (see Table 7). This is consistent with a peculiarity of the Japan Sea deep-water fauna characterized by Nishimura (1966b, pp. 135–136) that it consists almost exclusively of such animals that are primarily inhabitants of the littoral system. On the other hand, the fact that half of the mentioned fauna “in the truly deep waters” (sensu Nishimura, 1967, p. 352) is occupied by southern group species is incompatible with the conclusion given by Nishimura (1967) that “the deep water fauna.... of the Japan Sea is composed exclusively of the truly cold-water elements of northern affinity.” According to Nishimura’s (1974, pp. 177–182; 1982a, p. 388) speculation, such cold-water littoral species “have adapted to low temperature and then penetrated into the deep-sea environment in comparatively recent geological time.” Available information to deal with this inconsistency is still poor. These eurybathic warm-water ascidians are surprisingly adaptable to deep environment filled with the Japan Sea cold water mass that is “significantly colder (0.1–1.0°C) than those of the East China Sea (4–6°C) and the Okhotsk Sea (1.8–2.5°C)” (Nishimura, 1982a, p. 388; also see Nishimura, 1973, pp. 174–177). This great adaptability is suggested by the fact that the eurybathic and warm-water ascidians *Pyura lepidoderma* and *Halocynthia hispida* are also known from embayments, where environmental conditions generally show extreme variability. From the lack of benthic foraminiferan tests in the piston-core samples taken from the bottom of the Japan Sea at depths of 935 to 1115 m, it is inferred that basins of the Japan Sea deeper than at least about 1000 m had been filled with almost anoxic water that killed benthic biota around the later part of the last glacial period (see Arai et al., 1981; Oba, 1983; Oba et al., 1984). This conclusion is supported by the discovery of layers with extremely high sulfur contents in the piston-core samples collected from 2360 to 3540 m deep in the Japan Sea, which is considered as a result of hydrogen sulfide-bearing water (Masuzawa, 1983; Masuzawa & Kitano, 1984). In this connection, the formation of the bathyal and abyssal topography of the present Japan Sea may trace back to the beginning of the Pleistocene (Ujiié, 1982) or Pliocene (Fujita & Ganzawa, 1982), and therefore, may be far older than the mentioned extinction. Favorable conditions for life there are estimated to have reappeared about 20,000 years ago based on <sup>14</sup>C ages by Oba (1983) and Oba et al. (1984), while 13,000 years ago on the basis of widespread tephra by Arai et al. (1981), Masuzawa & Kitano (1984) and Masuzawa (personal communication). According to Oba et al., the extinction was followed first by the recruitment of northern-group organisms conveyed by the Oyashio, and then the southern-group ones began to spread into the Japan Sea by the Tsushima Current about 10,000 years ago. However, Ogasawara (1981) suggests the “influxes of warm water from the south through the Paleo-

Tsushima Strait" (p. 10) during the late Late Miocene to Late Pleistocene, especially interglacial stages, on the basis of paleontological studies of shallow-water molluscs. Thus, the eurybathic warm-water ascidians may have joined deep-water fauna of the Japan Sea and may have adapted themselves to the cold environment only in these 10,000 to 20,000 years.

Another deep-water ascidian, *Pelonaia corrugata bursaria*, a northern OB element, is found in the northern part of the Japan Sea at depths of 4 to 900 m, in contrast to 503 to 1366 m in the Okhotsk Sea. On the other hand, its nominotypical subspecies which is reckoned as an ANA element has been recorded from these two regions at depths of 0 to 200 m. Thus, in the Okhotsk Sea the subspecies *bursaria* may have been segregated in habitat from the nominotypical one as such to live in the deeper but mostly warmer water-mass, while the nominotypical one inhabits the shallower but usually much colder water inclusive of so-called dichothermal water. In the Japan Sea, the cold-adapted nominotypical subspecies is restricted to the littoral zone, while *bursaria* inhabits that zone and also extends for deeper into the Japan Sea cold water mass. The distribution patterns of these two subspecies, especially the occurrence of *bursaria* in the Okhotsk Sea, is not explained by Nishimura's hypothesis.

The following three species are found exclusively in deep waters in the Japan Sea: *Aplidium rhabdocormi*, *Agnesia orthenteron* and *Megalodicopia hians*. The first two are respectively quite similar in structure to their congeners inhabiting the littoral areas, but the last is a member of the monotypic genus of the exclusively deep-water, much deformed family Octacnemidae. Following Nishimura's (1967) hypothesis, in morphological features, the first two may be regarded as secondary deep-water animals, while the last is a primary one. *M. hians* is of special interest because the deep-water fauna of the Japan Sea has very few primary deep-water animals (Nishimura, 1974). *A. rhabdocormi* flourishes in the Japan Sea in several areas, down to 1410 m deep (see the description of this species), as well as off Kagoshima, 300–380 m, while *A. orthenteron* has been recorded only once from the Japan Sea at a depth of 1900–2090 m. In short, these two secondary deep-water ascidians are endemic to the Japan Sea and its vicinity, inhabiting in the Japan Sea the "Japan Sea cold water mass". Putting aside phylogenetic analyses, if Nishimura's (1974) considerations are followed, these two species are assumed to be derived each from a mother species dwelling in littoral areas of northern seas, and to have originated on the bottom under the cold water mass, then maintaining each population exclusively within the water mass, as may be the case with a polychaete *Harmothoe derjugini* Annenkova, 1937 (Nishimura, 1966a). As mentioned above, the basins of the Japan Sea deeper than at least about 1000 m are considered to have been deprived of most metazoans including ascidians until 13,000 or 20,000 years ago. Thus, the origin of these two genuine deep-water ascidians may date back to 20,000 years or less ago. Such a short period might be insufficient for speciation, but several examples of rapid speciation are available (Briggs, 1974; Stanely, 1979), which "by partial or complete physical isolation, must have begun only a short time ago (in the order of 1,000 to 10,000 years or less)" (Stanley, 1979); an extremely short case is that "the planktonic copepod *Cyclops dimorphus*

seems to have appeared in less than 30 years." The genus *Aplidium*, comprising more than 200 species inclusive of many unascertained ones (Nishikawa, 1986e), is under active speciation. This suggests a recent origin for *A. rhabdocormi*, if following Nishimura's (1982b) "stage theory of phylogeny." On the other hand, the family Agnecidae and the genus *Agnesia* contain a limited number of species throughout the world (13 species in the genus and 25 in the family; see Nishikawa, 1986e, and revised by subsequent studies). This fact makes me hesitate to attribute "youthfulness" to *A. orthenteron*, and therefore, its origin may not be covered by Nishimura's hypothesis.

The primary deep-water ascidian *M. hians* occurs widely but sporadically in the Japan Sea (366 m), Sagami Bay (350 m), the Weddel Sea (810–1555 m), and the Peru-Chile Trench (5325 m), though the identification of the last record is doubtful. The related genera *Dicopia* and *Situla* are known also from various deep-sea floors, and the center of origin of this group is not presently known. In the Japan Sea *M. hians* is confined to the transitional zone at a depth of 366 m, north of Sado Island, where the water temperature is 3–4°C in summer, and about 1°C in winter (Nishimura, 1969, pp. 70–77), and this temperature is more or less warmer than that in the Japan Sea cold water mass below this zone. This habitat is similar to that of the primary deep-water invertebrates that inhabit not truly deep waters but moderate depths around the edge of the continental shelf in the Japan Sea and are "all of the tropical-subtropical origin or affinity" (Nishimura, 1967, p. 352). These primary deep-water animals may represent the descendants of the warm-water littoral species that flourished between the Cenozoic and the first half of the Neogene when the earth had wholly a benign climate (Nishimura, 1974). If this is applicable to *M. hians*, its limited occurrence in depth in the Japan Sea is the result of warm-water origin or affinity, and it is not cold-adapted to inhabit the Japan Sea cold water mass. If the disjunct pattern of distribution in this species shown above is regarded actual, this primary deep-sea ascidian may be now at the shrinking stage of distribution (see Nishimura, 1982b, pp. 193–197). If these are admitted, and further, like other ascidians, *M. hians* does not have a long distance dispersal stage, then its population in the Japan Sea may well be regarded as a relict one, surviving to the present day beyond such catastrophic events as shown above. This ascidian may have survived in the narrow zone between the surface diluted water (see Arai et al., 1981) and deeper anoxic one, as suggested generally by Horikoshi (1987) (also see Nishimura, 1974).

(D) Littoral ascidian fauna of the Japan Sea and the east Asiatic endemic species

In the ascidians, there appear to be no valid taxa superior to the species level, that are endemic to east Asiatic waters, but many endemic species are known from these waters. The species belonging to the SJ, JPN and JS groups are all endemic to east Asiatic regions and are thriving to varying degrees in the Japan Sea. As shown in Table 7, the SJ species are most abundant and widespread, followed by the JPN and the JS species. Some of the JPN species are recorded from many districts, while many of the JPN and all the JS species except *Chelyosoma siboga* are found only sporadically. All the genera to which ES ascidians belong are fairly common,



each containing a considerable number of species recorded widely, except the genus *Syndiazona* that includes only a SJ and a WP species. Following Nishimura's (1974, 1981) criterion distinguishing initial endemism from relict endemism, all the mentioned EA ascidians are here considered as of the initial endemism in the east Asian seas. Namely, the ascidians may have originated in the Paleo-Japan or Paleo-East China Sea. If this is admitted, most JS ascidians are at a very early stage of initial endemism, while the SJ ones are at their expansion stage, and the JPN ones at an intermediate stage between these two. Among the SJ ascidians, *Syndiazona grandis* does not seem to be thriving, as is seen from Table 7, but this probably reflects inadequate sampling, because this ascidian was listed as a leading species of the "Okaba" community II "met with most frequently and abundantly in the eastern and southern bottom of the Japan Sea" (Nishimura, 1966a, pp. 373-374). All the SJ species except this are usually found in embayment-like environments. The most prevalent species among the SJ ascidians is obviously *Halocynthia roretzi*.

Regional infraspecific differentiation, such as those reported by Horikoshi (1976) for a gastropod species *Omphalius pfeifferi* (Philippi, 1846) and a bivalve *Chlamys farreri* (Jones et Preston, 1904) between the populations of the Japan Sea and of Pacific coasts of Japan, is not recognizable in ascidians.

(D1) Littoral ascidians endemic to the Japan Sea

Of the 32 species endemic to the Japan Sea, many are of uncertain identity and present much difficulty in determining their respective mother-tribes, except for the two species of *Chelyosoma* to be mentioned below. As already stated, all the JS ascidians except *Chelyosoma siboja* occur very sporadically throughout the littoral areas of the Japan Sea; their apparent abundance in Mutsu Bay, Oki Islands region and Peter the Great Bay (see Table 7) may be due to comparatively large sampling efforts. *Chelyosoma siboja* is recorded from many localities along the Japanese and Korean coasts of the Japan Sea. Records of many JS ascidians hitherto exclusively along the coast of Honshu is unexpected in view of the trend of distribution of the organisms endemic to the Japan Sea, as suggested by Nishimura (1966b). Basing largely on the fishes, he states that the littoral biota of the temperate and subtropical region of the Japan Sea contains very few JS organisms, while that of the subarctic region includes many, with northern affinities. From this trend, Nishimura (1982a) concluded that the basin "in the Japan Sea may have been completely isolated or connected with the ocean only by a narrow (northern) channel, possibly situated across present-day southern Hokkaido" (p. 390), instead of by a "southern channel" across present-day Tsushima and Korea Straits even in the interglacial periods, from the Late Pliocene through the Pleistocene. Nishimura (1974) claims that, if the Japan Sea basin had been connected with warm water by the "southern channel", more endemic species derived from warm-water tribes should be found. Thus, if the above-mentioned peculiar distribution of JS ascidians means that they were derived from warm-water tribes, Nishimura's conclusion needs reconsideration. This supposition may, however, be discarded by the information that *Chelyosoma siboja*, the most thriving ascidian among the JS species and inferred to be derived from the

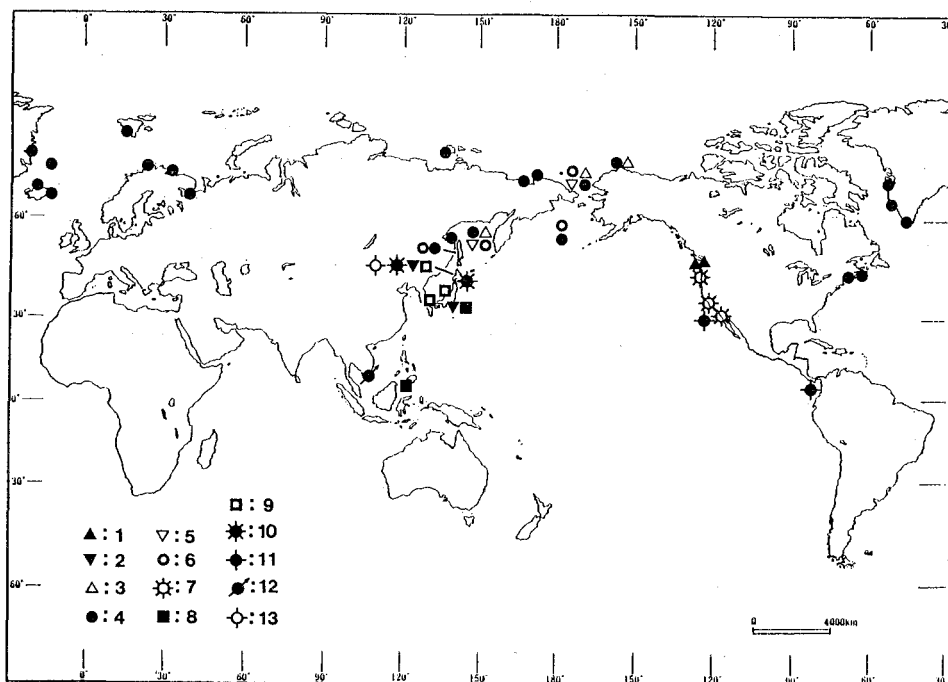


Fig. 44. World-wide distribution of all the recorded species of the genus *Chelyosoma*. 1: *C. columbianum* Huntsman. 2: *C. dofleini* Hartmeyer. 3: *C. inaequale* Redikorzev. 4: *C. macleayanum* Broderip et Sowerby. 5: *C. ochotense* Redikorzev. 6: *C. orientale* Redikorzev. 7: *C. productum* Stimpson. 8: *C. sibogae* Sluiter. 9: *C. siboga* Oka. 10: *C. yezoense* Oka. 11: *Chelyosoma* sp. described by Van Name (1945, p. 209). 12: *Chelyosoma* sp. by Dawydoff (1952, p. 152). 13: *Chelyosoma* sp. in the present study.

cold-water tribe (see just below), inhabits cold temperate to warm waters, but not subarctic region.

Fig. 44 shows the distribution of all 13 known species of *Chelyosoma*, including 3 unascertained ones. Out of these 13 species, 6 are known from the northern part of the Japan Sea, 4 from the Okhotsk and the Chukchi Sea, while 3 from the west coast of North America. If *Chelyosoma* is regarded as at the pandemic stage of Nishimura (1982b), it is logical to infer that the center of phyletic differentiation of the genus is located at a place where most species exist (according to Wallace's (1880) theory, see Nishimura, 1974), that is, the northern part of the Japan Sea or the Okhotsk-Bering-Chukchi region. Thus, all the EA species of *Chelyosoma* recorded from the Japan Sea, i.e. *C. siboga*, *Chelyosoma* sp., *C. dofleini* and *C. yezoense*, are of the northern group; the first two are endemic to the Japan Sea, while the last two are found on the Japan Sea and Pacific coasts of Japan, though less abundant than *C. siboga* in the Japan Sea.

(D2) Littoral ascidians endemic to Japanese waters, and the "amphi-Japanese disjunct distribution"

As is shown in Table 7, being indicated by JPN, 42 species are considered to be

endemic to the Japanese waters. Of these, inferred from the distribution patterns of respective close-relative taxa, 7 species are assumed to be of northern group and 4 are of southern group, leaving the rest of uncertain derivation. *Ascidia zara* and *Polycarpa cryptocarpa kroboja* are the representatives of northern and southern affinity, respectively, thriving on both the Japan Sea and Pacific coasts of Japan.

According to Nishimura (1971, and elsewhere), the species of southern affinity may have originated from Indo-West Pacific mother species isolated in the Paleo-East China Sea or Paleo-Japan Sea during glacial stages at the end of Neogene and the Pleistocene; thus, the species almost always inhabit estuaries or shallow-water embayments (Nishimura, 1981). Among the 4 JPN species of southern affinity, only *Polycarpa doederleini* appears to prefer, though not exclusively, such environments. Another southern ascidian *Polycarpa cryptocarpa kroboja*, which may be most reliable in the inference as to affinity among the 4 species because its nominotypical subspecies is found widely from the Indo-West Pacific region, does not seem to inhabit such environments. The mode of speciation might be somewhat different, as discussed by Matsukuma (1986) on the origin of some Japanese-Korean endemic glycymeridid molluscs, from that generalized by Nishimura's hypothesis mainly on the basis of crabs and sea-urchins.

Among the 7 JPN ascidians of northern affinity, *Ascidia zara* has its close relatives exclusively in the western coast waters of North America and *Cnemidocarpa miyadaii* has in the North Atlantic. The respective relatives are found in the Arctic and the boreal North Pacific for *Cnemidocarpa fertilis fertilis*, *C. fertilis minor*, *Chelyosoma dofleini* and *C. yezoense*, and in the Okhotsk-Bering for *Styela clava symmetrica*. The origin of these species may be inferred in several ways (see Nishimura, 1971, pp. 177-178; 1981, pp. 232-233, 235-236).

Generally speaking, most of JPN species are roughly equally abundant on both the Japan Sea and Pacific coasts of Japan: in contrast, *Didemnum translucidum*, *Clavelina elegans* and *Polycarpa granosa* are abundant on the Pacific coast but rather rare on the Japan Sea coast, being restricted to southern-most districts, while *Didemnum pardum*, *Styela clava symmetrica*, *Halocynthia turboja*, *Microsasmus multitentaculatus* and *Molgula xenophora* show the reverse and are known on the Pacific side exclusively from a single or two distant areas so far.

Figure 45 shows the distribution of the 17 JPN species which are found in the Japan Sea, whether abundantly or not, and are also recorded on the Pacific coast from a limited region, evidently far distant from the population in the Japan Sea. Such a remarkably discontinuous distribution pattern is called here the "amphi-Japanese disjunct distribution." An extreme case is seen in *Leptoclinides rugosum*, *Ascidia armata* and *Halocynthia turboja*, which are known on the Japan Sea coast from the middle of Honshu (from Sado and Niigata to Wakasa Bay) and on the Pacific coast from Sagami Bay.

Amphi-Japanese disjunct distribution is also discernible in other kinds of animals; two stony corals, *Rhizopsammia minuta mutsuensis* Yabe et Eguchi, 1982 and *Oulangia stockesiana miltoni* Yabe et Eguchi, 1932, are examples, both of which are endemic to the

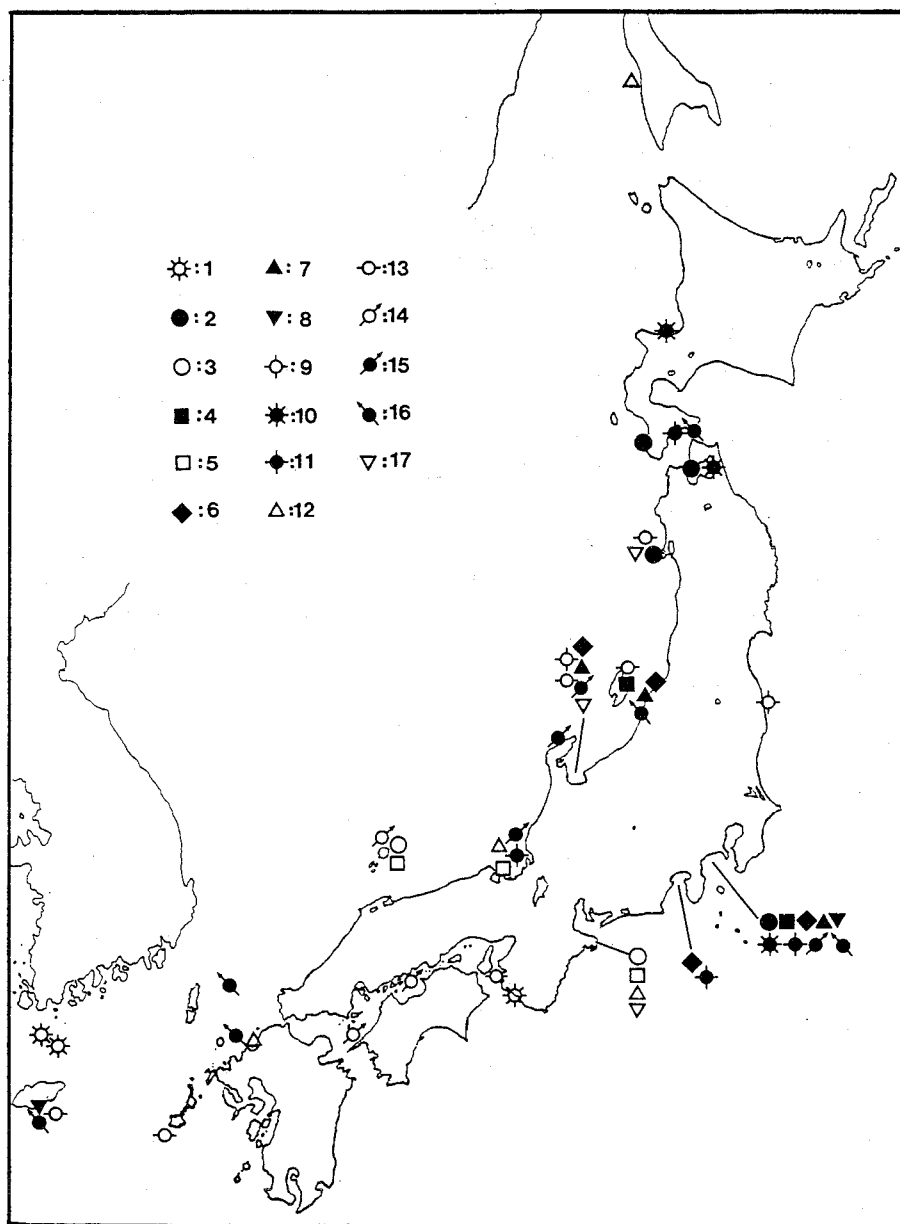


Fig. 45. Distribution of the 17 ascidians endemic to the Japanese waters and with restricted occurrence on the Pacific coasts. 1: *Pseudodistoma antinboja* Tokioka, 2: *Didemnae* (*D.*) *pardum* Tokioka. 3: *Leptoclinides komaii* Tokioka. 4: *L. rugosum* Tokioka. 5: *Ascidia matoya* Tokioka. 6: *A. longistriata* Hartmeyer. 7: *A. armata* Hartmeyer. 8: *A. zyogasima* Tokioka. 9: *Adagnesia vesiculiphora* Nishikawa. 10: *Chelyosoma dofleini* Hartmeyer. 11: *Polycarpa psammotesta* Tokioka. 12: *Cnemidocarpa miyadaii* Tokioka. 13: *Styela clava symmetrica* Tokioka. 14: *Halocynthia igaguri* Tokioka. 15: *H. turboja* (Oka). 16: *Molgula xenophora* Oka. 17: *M. oligostriata* Tokioka.

Japanese waters. *R. minuta mutsuensis* is so far known on the Japan Sea coast northerly from Shakotan Peninsula, middle Hokkaido, southerly to Wakasa Bay, while on the Pacific side exclusively from Sagami and Suruga Bay (Suzuki, 1969; Yajima, 1986). *O. stockesiana miltoni* is known from Mutsu Bay and around Tobishima and Sado in the Japan Sea and from Oofunato area and Sagami Bay on the Pacific side (Suzuki, 1969).

How has the amphi-Japanese disjunct distribution appeared? One possible speculation is that the population on the Pacific coasts may have been derived from the Japan Sea population by a branch of the warm Tsushima Current all over northerly through Tsugaru Strait and then southwards along the Pacific coast first by the cold Oyashio Current and finally by the Oyashio Undercurrent (see Omori & Tanaka, 1967; Omori, 1967). However, the submerged Oyashio Current beneath the warm Kuroshio Current may be limited in Sagami Bay and Suruga Bay to the pelagic layers deeper than at least 200 m (see fig. 2 of Omori, 1967) and usually 400 m (Omori & Tanaka, 1967), and influence the bathyal (deeper than about 500 m) benthic fauna (Okutani, 1972). Thus, if recruitment of the daughter population through the Oyashio Undercurrent is presumed, this speculation is applicable only to animals occurring on the Pacific side on the deep-sea floor, such as *Megalodictyon*, and never to the littoral organisms in question.

Other considerations may be also possible in view of the geological history of the Japan Sea area and the island-arc surrounding it. It has remained a subject of bitter controversy when and how the Japan Sea originated (for review see Kaseno, 1975, 1982, Ujiie, 1982; Kobayashi, 1983; Kimura, 1985). Here, I will briefly refer to the knowledge on the marine fossil fauna found on the Japan Sea coasts of Japan, starting with the Kadonosawa fauna (16.5–15 Ma ago, according to Tsuchi, 1986a, b).

According to Ujiie (1982), as inferred from micropaleontological and sedimentological studies, "the first invasion of sea water into the region (=the Japan Sea) may have occurred in the earliest Middle Miocene" (p. 407) along the Japan Sea coast of the Japanese islands. If this event was accompanied by the opening of the Japan Sea through the back-arc spreading between the Japanese islands and the Asian Continent, Ujiie's dating may be consistent with conclusions as to the timing of the opening drawn from recent paleomagnetic data (Haysahi & Ito, 1984; Otofujii et al., 1985; Torii et al., 1985; Hamano & Tosha, 1985; but for criticism see Kimura, 1985). Following Ujiie's dating, one of the youngest estimates of this sea, the first littoral fauna can be found in the warm-water Kadonosawa fauna. The warm-water environment in the Japan Sea may be due to the remarkable inflow of the Kuroshio Current proper into the sea through Tsushima and Korea Strait at that time (Chinzei, 1981; Chiji, 1986; Itoigawa & Shibata, 1986), though passages of the inflow are considered otherwise (Fujoka et al., 1981; Ujiie, 1982). At any rate, according to Tsuchi (1986a,b) and Chinzei (1986a,b,c), the majority of the Japanese islands were occupied by the warm-water Kadonosawa fauna, except the northern half of Hokkaido which was inhabited by cold-water Chikubetsu fauna, and the mixing

area of southward cold current with northward warm current (Kuroshio) may have occurred around the middle Hokkaido on both the Japan Sea and the Pacific coast (Chinzei, 1981 and elsewhere). The cold-water *Portlandia tokunagai* association is nearly contemporary with the Kadonosawa fauna and is found widely from northern areas of Japan southerly to central Honshu; this association is considered by Chinzei (1981) to represent the existence of the southward cold undercurrent beneath the northward warm current mentioned above. At about 15 Ma ago, however, the Kadonosawa fauna was suddenly replaced by temperate to subarctic Shiobara-Yama fauna (15–10 Ma) on the Japan Sea coast of the whole Japanese islands and the Pacific coast of northeast Honshu and Hokkaido. This may be attributable to the closure of Tsushima Strait that prevented the inflow of Kuroshio Current into the Japan Sea and led it to the sea in which the southward cold current predominated, though sometimes the northward warm Kuroshio Current may have invaded into the Japan Sea through the strait (Kaseno, 1975). The southward cold current flowed into the sea (or the gulf) through the northern channel situated presumably on the Tomakomai Depression of central Hokkaido (Ujiié, 1982). The Shiobara-Yama fauna was followed by likewise temperate to subarctic Omma-Manganji fauna (5–1 Ma) after a long non-fossiliferous period. This fauna also contains some warm-water bivalves, that suggests the presence of inflow of the Kuroshio into the Japan Sea through Tsushima Strait (for further details see Ujiié, 1982; Ogasawara, 1981). However, constant inflow is considered to have begun at about 1 Ma ago on the basis of analyses of warm-water pelagic foraminiferan fossils (Ibaraki, 1986), though inflow at the present rate may date only to the earliest Holocene (Ujiié, 1982) about 8,000 years ago (Oba, 1983; Oba et al., 1984). Until that time, the Japan Sea may have remained more or less stagnant, covered usually with cold and low-salinity surface water, with an oxygen-poor sea floor. Especially around the later part of the last glacial period, the sea bottom may have been so short of oxygen that most benthic animals could not survive, until remarkable inflow of the cold Oyashio Current began through Tsugaru Strait (Oba, 1983; Oba et al., 1984). On the other hand, on the Pacific coast of southwest Japan, the warm-water Sagara fauna appeared at about 12 Ma ago after a long hiatus; by this time, the present-day boundary between Kuroshio and Oyashio Current, situated off Choshi, Boso Peninsula, was established. The Sagara fauna was succeeded by the Kakegawa fauna which lasted until 1 Ma ago, and from it the main part of the recent Kuroshio fauna may have developed (Tsuchi, 1986b, p. 41). Izu Peninsula is supposed to have moved north with the Philippine Sea floor to join the middle of Honshu island at about 5–3 Ma ago, as inferred from paleomagnetic data (Hirooka, 1984, 1986; also see Seno & Maruyama, 1984); thus, the present-day Sagami Bay and Suruga Bay appeared. The northeast and southwest parts of Japan are believed to have been separated from each other about 20 Ma ago on the basis of marine deposits dating from this age on the Fossa Magna region (Fujita, 1985); the connection of the Japan Sea with the Pacific Ocean through this region is considered to have continued until the end of the Miocene (about 5 Ma ago), according to Prof. Hiroshi Shibata of Nagoya University and also according to the estima-

tion that "the Omma-Manganjian fauna was first established through upheaval of the Japanese Islands, when a distinct barrier between the Sea of Japan and the Pacific Ocean was first established" (Ogasawara, 1986, p. 238).

The occurrence of the amphi-Japanese disjunct distribution pattern seen in some littoral animals is inferable from the above-mentioned historical outline of the Japan Sea, as well as from the reconstructed paleogeography of Japan given by Chinzei (1986b, text-fig. 2), Ogasawara (1986, test-fig. 2) or others. This distribution pattern is best accounted for by the speculation that the mother population once inhabiting the Fossa Magna region was split into the Japan Sea and Pacific daughter populations by land emerging after the end of the Miocene. This can be a more defendable hypothesis than the disappearance of the larger part of a single population once distributed widely around the southern or northern half of the Honshu island with only two small parts of the population surviving up to now, one along the Pacific coast of central Honshu and the other along the Japan Sea coast. In the former speculation, namely the disjunction model, the two daughter populations are assumed to have remained since the time of splitting in spite of subsequent vast environmental changes in the last 5 Ma.

In the disjunction model, the mother population is considered as the species of initial endemism originating either to the south or to the north of the Japanese islands. In the former case, the mother population is regarded to have been brought into the Japan Sea, and to the Pacific coast of Japan, by the Kuroshio Current and inhabited the Fossa Magna region as a member of the Kadonosawa fauna in the early Middle Miocene (16.5–15 Ma). In the latter case, the population may have moved to the Fossa Magna region as a member of Shiobara-Yama fauna in the Middle Miocene (15–10 Ma). Other speculations are also possible as to the origin of the mother population in question, that it may have originated within a single water-mass formed in the mixing area of the cold and warm currents; the water-mass may have occurred on the coasts of middle Hokkaido in the early Middle Miocene (16.5–15 Ma) and immigrated as a single population southerly to the Fossa Magna region with southward shift of the border between the cold and warm currents at about 12 Ma ago; or the mass occurred around the Fossa Magna region in the Middle Miocene (15–10 Ma). The mixing area might also have been on the boundary between the cold undercurrent and superficial warm current; the boundary would correspond roughly to the bottom areas just underneath the southern limit of the undercurrent, and is considered in the early Middle Miocene to have been located around the central Honshu (see fig. 2 of Chinzei, 1981). Thus, the mother population of an amphi-Japanese species is derivable from either the warm- or cold-water tribe. For the above-mentioned speculation on the origin of the amphi-Japanese species in the water-mass around the Fossa Magna region, Ogasawara's (1986) inference as to the origin of the Omma-Manganji fauna may be highly suggestive from the systematic viewpoint. He says that "at least some elements" of the fauna "were derived from the fauna of Shigarami Formation" located in the northern part of Nagano Prefecture, belonging to the northern Fossa Magna region, and "may represent a somewhat ear-

lier fauna than the Omma-Manganzian fauna."

In the disjunction model, the two daughter populations are assumed to have remained unchanged morphologically even after long isolation. Perhaps, a strong support for this assumption can be sought in the marine animals known as ampho-American species. As is explicitly explained by Briggs (1974, 1984), some species of tropical marine fishes, crabs, sponges, trematodes and echinoderms exclusive of echinoids "can still be considered identical" on each side of the Isthmus of Panama, showing ampho-American disjunct distribution. In other words, in these species "specific differences have not yet developed" since "the isthmus connection between North and South America was completed about three to five million years ago" (Briggs, 1984, p. 431). This split the single mother population into the eastern Pacific and western Atlantic daughters. Moreover, the period of 5 Ma can not simply be regarded as an extraordinarily long species duration, because the average is estimated to be 5–7 Ma in echinoids, 10 Ma in marine gastropods and 20 Ma in reef corals on the basis of fossil records (see Stanley, 1979, fig. 9–2, pp. 231–258). Unfortunately the rate of phyletic differentiation in ascidians has not yet been inferred from the fossil records because of the general lack of fossils and genetic distance has not been estimated among the extant species. However, I believe that the disjunction model proposed here can become a hopeful hypothesis. It should be tested from various viewpoints.

#### Acknowledgements

I would like to express my deep and heartfelt gratitude first to Dr. Takasi Tokioka, Former Director of SMBL of Kyoto University, who kindly introduced me to ascidian taxonomy, gave me much valuable advice, support and encouragement beyond description, and read the manuscript critically. Hearty thanks are also due to the support and encouragement by Profs. Hiroshi Watanabe of the University of Tsukuba, Yukio Iwaikawa and all my other colleagues, Saburo Nishimura of Kyoto University, Eiji Harada of SMBL, Takeshi Yanase of Osaka Kyoiku University and Shigeko Ooishi of Mie University, as well as Drs. Minoru Imajima of NSMT and Ken-ichi Ôgi, Prof. Emeritus of Nagoya University. Profs. Harada and Nishimura, late Dr. Tatsunori Ito of SMBL, and Prof. Charles and Dr. Gretchen Lambert of California State University kindly reviewed the manuscript. I am very grateful for assistance in my collecting materials to Drs. Masaki Takahashi and Nobuaki Takahashi of Marine Biomedical Institute of Sapporo Medical College, Dr. Takaharu Numakunai and other members of the Asamushi Marine Biological Station of Tohoku University, Mr. Rin'ichi Tokita and other members of the Fisheries Experimental Station of Akita Prefecture, late Mr. Tsutomu Shinya and other members of the Noto Marine Biological Station of Kanazawa University, Mr. Hiroshi Saito and others of the Oki Marine Biological Station of Shimane University, and the members of the Fisheries Research Station of Kyoto University, as well as to the Fishermen's Associations at the concerned areas along the Japan Sea coast of Hokkaido, especially to Messrs. Tsuyoshi Tani, Akira Munakata and Kintaro Ami of the association of Kabuka, Rebun Island. The following persons allowed me to examine many specimens collected mainly from the Japan Sea: Chitaru Oguro of Toyama University for the "Tansei-maru" collection; Koichi Sekiguchi, Tetsuo Iwami and Muneo Michikawa of the University of Tsukuba for the Oka collection; Tetsuo Kuwamura of Chukyo University; Teishichi Kobayashi of the Fukui City Museum of Natural History; Ryohei Yamanishi of the Osaka Museum of Natural History; Tohru Imaoka; Mieko Komatsu and Hitoshi Michibata of Toyama University; late T. Shinya and Masahiro Matada of Noto Marine Biological Station; Tohru Yasuda and Kenji Hibino of the Fisheries Experimental Station of Fukui Prefecture; Hisasi Yokoyama of Osaka City Institute of Public Health and Environmental Sciences; Taiji Kikuchi of Kyushu University; Shin-ichiro Fuse of Kyoto University; Makoto Fukumoto of Nagoya City University; Mitsuaki Nakauchi of Kochi University; Ta-



kaharu Numakunai of Tohoku University; Shohei Shirai; Michio Ootani; Yoshihiro Shirai and Kunihiro Yamamoto of Kanazawa Aquarium; Jun'ichi Kobayashi of Mitsubishi-Kasei Institute of Life Sciences; Kazuhiko Tsuneki of Shimane University; and Makoto Tsuchiya of the University of the Ryukyus. For loan of museum materials I am indebted to the kind courtesy given by the following curators: D. Kühlmann (MNB), Ailsa M. Clark and Gordon Paterson (BMNH), Linda Cole (NMNH), A. C. Pierrot-Bults (ZMA), Endra Willassen (ZMH), Erik Rasmussen (UZMK), Harold S. Feinberg (AMNH), late Hatsuki Tsujimura (BLIH), Minoru Imajima (NSMT) and Eiji Harada (SMBL). Drs. Claude and Françoise Monniot of Museum National d'Histoire Naturelle, Paris, Dr. Boon Jo Rho of Ewha Womans University, Seoul, and Dr. Craig M. Young of Harbor Branch Foundation, Inc., Florida kindly helped me to obtain information on some ascidians, Dr. Naoya Abe and Mr. Koichi Takenouchi of SMBL gave me useful information about some molluscs, and further, Drs. Hiroshi Shibata, Mitsuo Hoshino and Toshiyuki Masuzawa of Nagoya University offered useful suggestions as to the geological history of the Japan Sea and vicinity. This work is supported in part by Grants-in-Aid for Encouragement of Young Scientists from the Ministry of Education, Science and Culture, Japan (Nos. 57740416, 58740371 and 59740386).

[List of references are available in the first part of this serial paper (Publ. Seto Mar. Biol. Lab., 34, pp. 73-148).]

### CORRIGENDA

The second part of this serial paper (Publ. Seto Mar. Biol. Lab., 35, pp. 25-170): page 124, line 7, for "(1935)", read "(1945)"; page 124, in the explanation of Fig. 32, line 1, for "*atlantica* (Van Name)", read "*sigma* Hartmeyer".

---